The number of copulations of territorial males of the butterfly *Callophrys xami* (Lycaenidae)

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Abstract. The number of copulations by different males and in different territories was evaluated in the field in the butterfly Callophrys xami (Lycaenidae). The total number of copulations per male and per hour was very low (.0027 and .0029 copulations / male / h in 1989 and 1990, respectively). There was high variance among males in the number of copulations. Data from the few males observed copulating more than once suggests a mating advantage for big, long lived males. Variation among territories in the number of resident males, frequency of occupation and number of copulations suggests variation in territory quality. Frequency of occupation was not correlated with the territory variables measured, and there were no differences in any territory variable between territories in which copulations were observed and those in which no copulation was observed. Furthermore, there were no between-years correlations in frequency of occupation and number of copulations in the territories studied in two different years. The location of territories may be important in determining territory quality.

Key Words: Callophrys xami, Lycaenidae, copulation, mating success, territoriality

INTRODUCTION

The fitness of male insects is difficult to determine in the field (Thornhill and Alcock, 1983). Although the number of observed copulations has been used frequently as a measure of male fitness (Thornhill and Alcock, 1983), it is not possible to be confident about such a measure without knowledge of male mating costs, female copulation frequency, sperm competition pat-

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terns (Smith, 1984) and postcopulatory female choice criteria (Eberhard, 1996). However, some studies suggest that the number of copulations achieved by a male is an important fitness component at least in some species. One line of evidence supporting this suggestion is the fact that several aspects of the male phenotype seem to be specific adaptations to increase the number of copulations (reviews in Darwin, 1871; Thornhill and Alcock, 1983; Choe and Crespi, 1997).

In the butterfly *Callophrys xami* Reakirt (Lycaenidae) the number of copulations seems to be an important fitness component for males since they spend all their active adult lifetime defending territories that lack concentrations of larval and adult food resources (Cordero and Soberón, 1990) and that are used only as mating stations (Cordero and Soberón, 1990; Cordero, 1993). Laboratory observations suggest that copulation inhibits female sexual receptivity for a number of days (if it is the first mating of the female, these days correspond to the days in which oviposition rates are higher), and dissection of field collected females indicates a relatively low degree of polyandry (Cordero and Jiménez, unpublished data).

In this paper we report field observations of copulations by territorial males of the butterfly *C. xami*. Differences in the number of copulations performed by different males, and ocurring in different territories, are described and some factors possibly affecting such differences are discussed.

METHODS

The study was conducted in the Pedregal de San Angel ecological reserve, maintained by the Universidad Nacional Autónoma de México in the south of Mexico City. This zone is characterized by volcanic soil, rough topography, markedly seasonal rainfall regime, and xerophytic shrubby vegetation. *C. xami* is a multivoltine butterfly that can be found throughout the year at relatively low numbers, reaching its highest density from October to January (Soberón *et al.*, 1988). The main larval food plant in the study area is the perennial *Echeveria gibbiflora* (Crassulaceae), an abundant species (Soberón *et al.*, 1988; Larson *et al.*, 1994).

Study periods were chosen to coincide with population density "peaks" (Soberón et al., 1988; personal observation); observations were made between November 1 and December 20, 1989 and between November 10 and December 6, 1990. Most territorial males observed were captured and individually marked on the wings with felt-tip pens and their right forewing length was measured through the mesh of the net with a calliper (in the laboratory, male wing length is correlated with adult body weight at emergence: r = 0.91, p < 0.001, n = 28; Cordero, unpublished data). Individuals were assigned to one of three wing wear categories: (1) similar to a recently emerged adult (wings mostly green with intact margins), (3) very worn male (wings mostly brown with worn margins), and (2) all individuals intermediate between (1) and (3). Longevity was defined as the number of days elapsed between the first and the last observation of the male. Territory limits were determined as explained in Cordero and Soberón (1990). We measured the (i) maximum length and the (ii) "cross" length (length of the perpendicular axis crossing through the middle point of (i)); territory area was approximated as (i) x (ii); the ratio (i) / (ii) was used as a measure of territory "shape".

The study period of each year was divided in two parts. During the first part we

measured the frequency of occupation of each territory (= number of days the territory was occupied by a territorial male / number of days the territory was censused), determined the identity of each male defending the territory, and recorded all copulations observed. In this part of the study we made observations in 25 territories in 1989 and in 19 in 1990. One observer walked along transects joining several territories two times per day between 1000 and 1500 h, the daily territorial defense period (DTDP; Cordero and Soberón, 1990), during 31 days in 1989 and during 11 days in 1990, and observed each territorial male (if present) for at least two minutes. The observation period was longer if, for example, the male was interacting with a conspecific male or courting a female. The average number of days (\pm SD) each territory was censused was 26.2 \pm 1.8 (median = 26; range: 22–30) in 1989, and 10.2 \pm 0.6 (median = 10; range: 9–11) in 1990.

During the second part of each study period we estimated the probability of copulating twice in a day (previous work indicated that the maximum number of successful copulations per day that a male can achieve is two, since a male's first copulation of the day lasts 32 min on average, while the second copulation of the day lasts several hours; Cordero, 1993). We made focal observations of territorial males throughout the DTDP and recorded all copulations observed, during nine days in 1989 and 12 days in 1990. The number of males with focal observations was 15 in 1989 and 16 in 1990; the total number of hours of focal obsevations was 200 hours in 1989 (40 five hours periods of focal observations) and 130 hours in 1990 (26 five hours periods of focal observations). The number of days of focal observations per male varied from 1 to 6 in 1989 (mean \pm SD = 2.7 \pm 1.7, median = 2), and from 1 to 3 in 1990 (1.6 ± 0.8 , median = 1). Focal observations were made in 14 territories in 1989 and in 11 territories in 1990. The number of days of focal observations per territory varied from 1 to 6 in 1989 $(2.9 \pm 1.6, \text{ median} = 2)$, and from 1 to 3 in 1990 $(2.4 \pm 0.7, \text{ median} = 2)$ median = 3). All observations were made on sunny days since C. xami is not active under cloudy conditions. All summary statistics are given as mean ± standard deviation and/or median and range (minimum-maximum).

RESULTS

Throughout the study periods of 1989 and 1990, we observed territorial males (Cordero, 1997) and sexually receptive females. All successful courtships observed (n = 15) began inside territories and involved territorial males. Copulations were observed between 1100 and 1500 h in 1989 and between 1230 and 1500 h in 1990.

Number of copulations by different males

We observed a total of 27 copulations (Table 1). Although we marked and observed 159 territorial males (99 in 1989 and 60 in 1990), only 21 males (three of them unmarked) were observed copulating (12 in 1989 and 9 in 1990). Three males were observed copulating more than once (two, three and four times). Only one male was observed copulating two times in a day (this was the male that mated four times in 1989). We suspect that another male mated twice in one day (this was the male that mated three times in 1989), since this male was observed arriving at the territory at 1111 h and copulating at 1137 h for more than 268 min (observation was interrupted at 1605 h); therefore, it is possible that this male copulated before the begin-

	1989		1990 Number of copulations:			
Nur	nber of copu	lations:				
Т	First part	Second part	Т	First part	Second part	
3-4N	1	3ª	3-4N	0	1	
IV	0	2	IV	1	1 ^b	
Pnm	1	C	Pnm	1	0	
d	2	3^{d}	а	1	1	
Id	3	0	8-9	1	1	
V	1	0	A	0	1	
+	1	C	ICh2	0	1	

Table 1. Distribution of copulations observed in different territories in each part of the study periods of 1989 and 1990. T: territory.

^a Territory in which a male copulated twice in a day.

^b Although in this territory no focal observations were made, we casually observed one copulation during the second part of the study.

^c Territory in which no focal observations were made.

^d Territory in which a male probably copulated twice in a day.

ning of observations (focal observations began at 1004 and sometimes males began territory defense before 1000 h) and that the long copulation observed was the second of the day (remember that a male's second copulation of the day last several hours, while his first copulation of the day lasts on average 32 min). Therefore, only in one (possibly two) of the 40 five h periods of focal observations in 1989 we observed two copulations; no male copulating twice in a day was observed in any of the 26 five h periods of focal observations in 1990.

As expected from the different sampling methods employed during the first and second part of each study period, the proportion of marked males observed copulating in the first part of the study (10 / 144 = 6.9%; 8 / 92 in 1989 and 2 / 52 in 1990) was lower than the proportion observed copulating during the second part (10 / 31 = 32.3%; 4 / 15 in 1989 and 6 / 16 in 1990). Seven of the nine copulations performed by the three males observed copulating more than once were observed during the second part of the study (including the two copulations performed in the same day by a male).

The number of copulations per hour calculated from the pooled focal observations was similar in both years of study: 0.04 copulations / h (= 8 copulations / 200 h of focal sampling) in 1989 and 0.046 copulations / h (= 6 copulations / 130 h of focal sampling) in 1990. The number of copulations per male and per hour calculated from the pooled focal observations was almost identical in both years of study: 0.0027 copulations / male / h (= 8 copulations / 15 males / 200 h) in 1989 and 0.0029 copulations / male / h (= 6 copulations / 16 males / 130 h) in 1990.

Characteristics of males

A total of 99 territorial males in 1989 and 60 in 1990 were individually marked. No significant differences between years were found in wing length (1989: 1.64 ± 0.1 cm, range: 1.36-1.89, n = 90; 1990: 1.65 ± 0.09 cm, range: 1.4-1.83, n = 55; t = -0.29, p = 0.77), longevity (1989: 4.8 ± 5.1 days, median = 2, range: 1-20, n = 99; 1990: 4.9 ± 5.9 , median = 2, range: 1-28, n = 57; Mann-Whitney U = 2819, p = 0.99) and wing wear at the moment of being marked (1989: median = 1, range: 1-3, n = 90; 1990: median = 1, range: 1-3, n = 57; U = 2419.5, p = 0.51). There was no correlation between wing length and longevity (1989: $r_s = 0.13$, p = 0.22, n = 90; 1990: $r_s = 0.11$, p = 0.43, n = 52).

Due to the sampling methods employed in this study, we cannot look for a relationship between male traits and number of copulations in the data. However, the characteristics of the three males observed copulating more than once suggest that male size and longevity could be positively correlated with copulation success. The male with the most copulations (four) was also the biggest male observed in both years (wing length = 1.89 cm); this male was also the only one observed copulating twice in a day. The longevity of this male was 14 days, longer than that of 89.9% of the males observed in 1989. The male that was observed copulating three times in 1989 was bigger (wing length = 1.72 cm) than 73.3% of the males observed that year. The longevity of this male was 11 days, longer than that of 85.9% of the males observed in 1989. This male probably copulated twice in a day (see previous section). The male that was observed copulating two times in 1990 was bigger (wing length = 1.72 cm) than 74.5% of the males observed that year. The longevity of this male was 18 days, longer than that of 94.7% of the males observed in 1990. Therefore, the characteristics of the multiply mated males indicate that a study of the possible (positive) effect of wing length and longevity on male mating success would be particularly interesting in this butterfly (see Appendix).

Number of copulations in different territories

The 17 copulations of 1989 and the 10 copulations of 1990 were observed in seven territories each year, although only three of these were the same in both years (Table 1). To explore the relation between territory variables (maximum length, "cross" length, maximum length / "cross" length and area) and the frequency of occupation of the territory, and to compare the characteristics of territories in which copulations were observed with those in which no copulations occurred, only the data obtained during the first part of the study periods were analized. This decision was made considering that during the second part of both study periods the sampling effort was very heterogeneous (the number of days of focal observations per territory varied from 1 to 6 in 1989 [CV = 55.2%] and from 1 to 3 in 1990 [CV = 29.2%]), whereas during the first part of both study periods it was much more homogeneous, and, therefore, comparable, between territories (the number of days each territory was censused varied from 22 to 30 in 1989 [CV = 6.9%], and from 9 to 11 in 1990 [CV = 5.9%]). Table 2. Comparison of characteristics of territories in which copulations were observed with those of territories in which no copulations were observed. Values are median (range). Statistics from Mann-Withney U test are given.

Territory variable	Year	Territories in which copulations were observed	Territories in which no copulations were observed	U	Þ
Maximum	1989	5.17 (2.69-6.2)	3.26 (2.32-7.1)	24.5	.2
length (m)	1990	3.81 (2.54-6.2)	3.88 (2.32-7.1)	19	.89
"Cross" length (m)	1989	3.27(1.5-4.35)	2.5 (1.35-4.85)	24	.19
0 ()	1990	3.02 (2.14-4.35)	2.68 (2-3.86)	17	.67
Maximum length /	1989	1.49 (.87-3.21)	1.16 (1.01-2.49)	31	.48
"Cross" length	1990	1.23 (1.03–1.84)	1.36 (1.01-2.25)	17	.67
Area (m ²)	1989	16.93 (7.21-26.97)	7.78 (4.54-33.61)	22	.14
. ,	1990	10.85 (6.22-26.97)	8.48 (4.56-27.41)	19	.54
Frequency	1989	.69 (.5292)	.33(.04-1)	21.5	.024
of occupation	1990	.85 (.64–.91)	.4 (0-1)	18	.36

^a This difference is not significant if we perform a sequential Bonferroni adjustment of significance levels using as a family of tests (Chandler, 1995) the five U tests of 1989, and using $\alpha = 0.1$, as suggested by Chandler (1995): k = 5, $\alpha/k = .02$.

Average frequency of occupation of territories during the first part of the study periods was 0.47 ± 0.29 (median = 0.5, range: 0.04–1) for 1989 and 0.6 ± 0.37 (median = 0.8, range: 0–1) for 1990. The frequency of occupation of territories was not correlated with any of the territory variables measured (Spearman correlations, all $p \ge 0.26$). Average number of copulations in territories during the first part of the study periods was 0.36 ± 0.76 (median = 0, range: 0–3) for 1989 and 0.24 ± 0.44 (median = 0, range: 0–1) for 1990. There were no significant differences between territories in which copulations were observed and territories in which no copulations were observed in maximum length, "cross" length, maximum length / "cross" length and area (Table 2). The frequency of occupation of territories in which no copulations were observed in 1989 (Table 2), but no difference was detected in 1990. However, even the 1989 difference is not significant if we perform a sequential Bonferroni adjustment of significance levels (see Table 2).

Twelve territories were observed in both years. Considering only the data collected during the first part of both study periods, there were no significant between-years correlations in the frequency of occupation of these territories ($r_s = 0.55$, p = 0.078, n = 11) or in the number of copulations (Gamma correlation, $\gamma = -0.09$, p = 0.87, n = 11) observed in these territories. Therefore, the "quality" of a territory in a given year was not a predictor of that in the next. In fact, the territory that in 1989 had the maximum number of observed copulations (five or, probably, six; Table 1) and the second highest frequency of occupation (0.94; maximum = 1), was not occupied by a territorial male in any of the more than 10 days in which it was censused in 1990.

DISCUSSION

Male copulation frequency

As is common in insects exhibiting lek territoriality (*e.g.* Alcock, 1983, 1987; Alcock and O'Neill, 1986; Table 3), the overall rate of copulations observed in *C. xami* was low: 0.0027 and 0.0029 copulations / male / h in 1989 and 1990, respectively. Low copulation rates are expected since lek mating systems are favored when receptive females are scarce and widely dispersed (Thornhill and Alcock, 1983; Rutowski, 1991), and such conditions seem to apply to the population of *C. xami* in the Pedregal de San Angel (Cordero and Soberón, 1990).

This study suggests that there was relatively high variance in copulation success between territorial males. First, although most males were not observed copulating, some males copulated up to four times, including one (probably two) male that was observed copulating two times in a day. Second, one third of the copulations observed (nine out of 27) were performed only by three males. Although we were not able to obtain estimates of male lifetime reproductive success, these results, together with information indicating that females exhibit a low level of polyandry (in a sample of 28 field collected females, 78.6 % had only one or no spermatophore in their corpus bursae, and the mean number of spermatophores found in non-virgin females was 1.37 ± 0.6 [Cordero and Jiménez, unpublished data]), suggests that there is high variance in male fitness and, therefore, that the opportunity for sexual selection in males is high. Sexual selection may be acting in favor of an increase in male wing length and longevity if the mating advantage suggested by the characteristics of the few males that mated more than once is real. However, the relationships between male phenotypic traits and copulation success still needs clarification.

Number of copulations and territory variables

The substantial variation observed between territories in frequency of occupation, numbers of males and number of copulations suggests that territories of *C. xami* vary in quality. However, none of the territory variables measured affected the frequency of occupation or the number of copulations (Table 2). In species with non-resource based territoriality, such as *C.*

Table 3. Mating behavior of butterflies in which male copulation success and/or phenotypic traits associated to male copulation success have been studied in the field ^a

Species	MS	ð MF	ð TSRMF	♀ MF ^b	♀ TSRMF	Reference
Papilionidae Papilio polyxenes	LT	.13 ± .49 (0-3) °	ST ^R	1.3 ± .54 (0-3)	WW ^R	Lederhouse (1981, 1982)
Atrophaneura alcinous	SC	$.43 \pm 1.31^{d}$ (0-5)	ED ^R , L ^R , ME ^R , WL ^{NR}	1.0	-	Suzuki & Ma- tsumoto (1992)
Luehdorfia japonica	SC	e	FA ^r , WW ^r , WL ^{nr}	~1.0 ^r	-	Tsubaki & Ma- tsumoto (1998)
Nymphalidae Coenonympha pamphilus	LT	.019 ^g .083	TB ^R , WL ^{pr}	$.97 \pm .05$ (0-3)	-	Wickman (1985)
Danaus plexippus	SC	2.98 ± 2.65 (0-11) ^{h, i}	FA ^{NR} , PL ^{NR} , WL ^{NR} ,WW ^{NR}	3.50 <u>+</u> 1.22 (1-6) ^j	FA ^R , PL ^{NR} , WL ^{NR} , WW ^{NH}	Frey <i>et al.</i> (1998)
Euphydryas editha	SC	^k	ED ^{NR}	1.27 ± .46 (1-2) ¹	-	Baughmann (1991)
Heliconius hewitsoni	РМ	Ξ.	BL ^R , WL ^R , WW ^{NR}	1.0	-	Deinert <i>et al.</i> (1994)
Pieridae C. philodice eriphyle	SC		G ^R	1.21 (0-3) ^m	WW ^{PR}	Watt <i>et al.</i> (1986)
Colias eurytheme	SC	-	G ^R	(3) ⁿ		Watt <i>et al.</i> (1986)
Pieris napi°	SC		PW ^R	2.03 ± .11 (1-5) ^p	-	Wiklund & Kaitala (1995)
Lycaenidae Jalmenus evagoras	РМ	$.97 \pm 2.56$ (0-7) ⁱ	L ^r , ED ^r , WL ^r	1.0	-	Elgar & Pierce (1988)
Callophrys xami	LT	.0027 (0-4) .0029 (0-2)9	WL ^{PR} , L ^{PR}	$1.37 \pm .60$ (0-3)	WL ^{NR} , WW ^{NR}	This study & Cordero (1998)

^a MS: male mating system according to the classification of Thornhill and Alcock (1983). LT: lek polygyny. PM: pupal mating. SC: scramble competition polygyny. MF: mating frequency. TSRMF: traits statistically related (^R), possibly related (^{PR}) or not related (^{NR}) to MF. BL: body length. ED: adult emergence date. FA: fluctuating asymmetry in forewing and hindwing radius length. G: genotype. L: longevity. ME: mating experience. PL: parasitism level. PW: pupal weight. ST: MF depends on specific territory. TB: territorial behavior (species with territorial and non-territorial males). WL: wing length (in the case of *L. japonica* this was measured as the forewing and hindwing radius length). WW: wing wear.

^b Mean ± SD (range) of spermatophore number of mated females.

^c Mean ± SD (range) for the second brood of 1975.

^d Mean lifetime number of copulations ± SD (range).

^e Number of matings estimated by assessing degree of scale loss from claspers.

^f Fifty out of 51 field collected females had one spermatophore and one had two (Matsumoto and Susuki,1995).

⁸ Number of copulations/ male/ census. Upper figure: non-territorial males; lower figure: territorial males.

^h Studied in a big outdoors mating cage.

ⁱ Mean lifetime number of copulations ± SE (range).

^j Pliske (1973), cited in Drummond (in Smith, 1984), estimated a mean number of spermatophores (maximum) = 2.23 (8).

^k Relative number of matings estimated by marking male genitalia with powdered fluorescent dye.

¹ Data from Ehrlich & Ehrlich (1978), cited in Drummond (in Smith, 1984).

^m Mean (range) (Drummond in Smith, 1984).

ⁿ Maximum number of spermatophores (Gwynne in Smith, 1984).

° Butterflies were raised in captivity and released in the field.

^p Mean ± SE (range).

^q Number of copulations / focal male / hour of focal observation (minimum number of copulations per male - maximum number of copulations per male). Upper figure: 1989 study period; lower figure: 1990 study period.

xami, it has been proposed that female "rules of movement" may be responsible for territory location and quality (Bradbury, 1985; Cordero and Soberón, 1990; Rutowski, 1991; Wickman *et al.*, 1995). Although female movement in *C. xami* has not been studied, casual observations suggest that territories are located in the confluence of natural or manmade trails, which are used by females for their displacement through the habitat (Cordero and Soberón, 1990). If this suggestion is true, differences in territory quality may result from the specific location of territories with respect to areas of high probability of female transit, which may vary with time (as suggested by the lack of between-years correlations in occupation frequency and number of copulations in territories).

Male copulation success in other butterflies

Field estimates of male copulation success are scant. In Table 3 we summarize the information on the mating behavior of butterflies in which male copulation success and/or phenotypic traits associated with male

copulation success have been studied in the field. Unfortunately, a formal quantitative comparison is prevented by the different methods employed to estimate copulation success (Table 3).

The copulation success of males has been shown to be affected by a variety of factors, such as weather conditions (Davies, 1978), adult emergence date (Elgar and Pierce, 1988), body size (Deinert et al., 1994; Elgar and Pierce, 1988), longevity (Elgar and Pierce, 1988), mating experience (Suzuki and Matsumoto, 1992), type of behaviour (territorial vs. non-territorial; Wickman, 1985), female mate choice (Rutowski, 1981-83) and fluctuating asymmetry (Tsubaki and Matsumoto, 1998). A positive effect of body size on male mating frequency has been found in two (four, if the possible cases of C. pamphilus and C. xami are true) species (Table 3): Jalmenus evagoras and Pieris napi; while in Heliconius hewitsoni body length is negatively correlated with mating success. The first species exhibits pupal mating, a mating system that involves direct male-male competition (the same as lek polygyny, the mating system of C. pamphilus and C. xami), the second species exhibit scramble competition polygyny, a mating system with indirect male-male competition, and the third species also exhibits pupal mating. These data suggest that big body size (or correlated traits) confer advantages in different male competition settings, although there may be situations in which small size may be advantageous, as in H. hewitsoni. However, in Atrophaneura alcinous (Susuki and Matsumoto, 1992) and Danaus plexippus (Frey et al., 1998), species showing scramble competition polygyny, no relation between male size and mating success was found. These observations are in accord with other studies that indicate that male size and resource holding power are correlated in some butterfly species (Rosenberg and Enquist, 1991) but not in others (Alcock, 1994). In the three species in which it has been investigated, a correlation between male longevity and number of copulations achieved has been found (Atrophaneura alcinous and J. evagoras) or is suspected (C. xami). These species have different mating systems, pertain to different families, and have very different adult body sizes (Atrophaneura alcinous is much bigger than the two lycaenids).

APPENDIX

A prospective comparison of all marked males observed copulating (CM) during the first and second parts of both study periods, with all marked males not observed copulating (NCM) supports the suggestion that copulation success may be correlated with wing length and longevity. CM had longer wing length (CM: 1.71 ± 0.1 cm, median = 1.72, range: 1.51-1.89, n = 14; NCM: 1.64 ± 0.1 , median = 1.65, range: 1.36-1.88, n = 131; Mann-Whitney U = 569, P = 0.0197) and lived longer (CM: 10.1 ± 5.6 days, median = 9, range: 2-20, n = 18; NCM: 4.1 ± 5 , median = 2, range: 1-28, n = 138; U = 397, P = 10^{-6}) than NCM, but the degree of wing wear at the moment of being marked was not different (CM: 1.4 ± 0.7 , median = 1, range: 1-3, n = 15; NCM: $1.6 \pm .7$, median = 1, range: 1-3, n = 132; U = 845.5, P = 0.29). The mean number of copulations of the CM was 1.3 ± 0.8 (median = 1, range: 1-4,

n = 18). We stress that these comparisons are based in data obtained from a heterogeneus, non-random, and probably biased sampling of males.

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